

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 108, No. 2

JUNE 1996

PAGES 205–396

Wilson Bull., 108(2), 1996, pp. 205–227

GEOGRAPHIC VARIATION AND SPECIES LIMITS IN *CINNYCERTHIA* WRENS OF THE ANDES

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ABSTRACT.—Few studies have quantified geographic variation in widely distributed Andean birds despite the fact that the linearity of their distributions provides unique opportunity to assess latitudinal geographic variation. We examined geographic variation of morphometric and plumage characters in populations currently treated as a single species, the Sepia-brown Wren (*Cinnycerthia peruana*), that inhabits humid montane forests from northern Colombia to central Bolivia. Our analysis supports the recognition of three biological species (*olivascens*, *peruana*, and *fulva*) based on discrete morphometric differences as well as marked plumage differences. Size variation within populations is inconsistent with the predictions of Bergmann's Rule, whereas variation across species runs counter to the predictions, with the smallest species occurring farthest from the Equator. *Received 20 June 1995, accepted 10 Dec. 1995.*

Before hypotheses concerning the origin and maintenance of geographic variation in bird species can be formulated, the patterns of variation must be well-described (Zink and Remsen 1986). Although the humid slopes of the Andes mountains are potentially one of the world's most productive areas for the study of geographic variation (Remsen 1984a, Graves 1985, 1988), few workers (e.g., Graves 1982, 1985, 1991, Remsen et al. 1991) have quantified geographic variation in widely distributed Andean birds. We present here an evaluation of morphometric and plumage variation in populations currently treated as a single species, the Sepia-brown Wren (*Cinnycerthia peruana*), that inhabits humid montane forests in the temperate and subtropical zones of the Andes from northern Colombia to central Bolivia (Fig. 1). We also re-evaluate species limits among these populations.

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The four currently recognized subspecies of *Cinnycerthia peruana* (*bogotensis*, *olivascens*, *peruana*, and *fulva*; Paynter 1960, Ridgely and Tudor 1989, Fjeldså and Krabbe 1990) were all originally described as distinct species based on size and plumage differences. Known only from the eastern Andes of Colombia, *bogotensis* differs from its geographically closest relative from the rest of the northern Andes, *olivascens*, by its darker coloration (Hellmayr 1934, Fjeldså and Krabbe 1990). Nominate *peruana* is smaller in size and less olivaceous than *olivascens*. Hellmayr (1934) noted that two of nine specimens from Ecuador had a faint greyish tinge in the postocular region; he interpreted this as revealing the close relationship between *olivascens* and *peruana*. It is not clear, however, whether Hellmayr realized that juveniles of *olivascens* typically have a grey postocular area. Hellmayr (1934) included the preceding taxa as subspecies within *Cinnycerthia peruana* but considered the most southern subspecies, *fulva*, to be a separate species (*C. fulva*) based on its distinctly smaller size and well-defined buffy-white superciliary. Until Hellmayr's (1934) revision, *fulva* was not considered to be congeneric with the other taxa (all in *Cinnycerthia*), but was placed in the genus *Thryophilus*. Paynter (1960) placed *fulva* as a subspecies within *C. peruana* and retained the other three subspecies; no reasons were published for the merger of *fulva* into *peruana*. Subsequent works on South American birds have followed Paynter's treatment (e.g., Meyer de Schauensee 1966, 1970; Ridgely and Tudor 1989; Fjeldså and Krabbe 1990).

METHODS

We examined six mensural characters with dial calipers (measured to the nearest 0.05 mm) on 235 (118 males and 117 females, according to gonad information on label) study skins: (1) wing-length (chord of unflattened wing from bend of wing to longest primary); (2) bill-length (of exposed culmen); (3) bill-width (at its base); (4) bill-depth (at its base); (5) tail-length (measured from point of insertion of central rectrices to tip of longest rectrix); and (6) tarsus length (from the joint of tarsometatarsus and tibiotarsus to the lateral edge of last undivided scute). In addition to the specimens at the Museum of Natural Science, Louisiana State University (hereafter LSUMZ), specimens were examined from five other museums with major collections of Andean birds (see Acknowledgments).

Specimens in juvenal or downy plumage or with damaged, extensively worn or molting wing and tail feathers were excluded. Because many specimens in "adult" plumage lacked data on age (e.g., skull pneumatization), we also performed separate analyses using only those specimens with skull pneumatization $\geq 90\%$ to determine the effect of inclusion of young birds

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FIG. 1. Distribution of *Cinnycerthia* taxa based on samples included in this study. Triangles are *bogotensis*, dark circles are *olivascens*, hollow circles are *peruana*, and squares are *fulva*.

in adult plumage. Similarly, most specimens did not possess data on body mass, a potentially useful size character. Using only specimens of known mass, an ANOVA was used to detect sex and subspecies differences. Mass was not used in the multivariate analyses.

Geographic coordinates for each locality were taken from Paynter et al. (1975), Paynter and Traylor (1977, 1981), and Stephens and Traylor (1983). SAS software (SAS Institute, Inc. 1982) was used to calculate all univariate statistics and perform regressions, analyses of variance (ANOVA, MANOVA), principal component analyses (PCA), and discriminant function analyses (DFA). Morphometric data were \log_{10} -transformed for all analyses to correct for a non-normal distribution. All ANOVAs were two-way a posteriori comparisons of least squares means with the rejection level set according to the number of comparisons by using the Bonferroni method.

Plumage colors of the 235 specimens were compared to a published color standard (Ridgway 1912) under a combination of fluorescent and natural overhead lighting. For *bogotensis*, *olivascens* and *peruana*, the postocular area of each specimen was scored as (0) no postocular stripe evident, (1) postocular stripe inconspicuous, poorly demarcated, and probably not visible in the field, or (2) postocular stripe conspicuous, reasonably well-defined, and probably visible in the field. For all specimens, the amount of white feathering on the head (in *fulva* group, excluding the superciliary) was scored as (0) none, (1) partial or complete, small, white eye-ring, (2) a portion of the forecrown with white feathers, (3) both 1 and 2, (4) extensive white feathering on face and forecrown, or (5) much of the head white, especially most of the face and crown. Because the degree of development of the superciliary and the extent of white feathering on the head are continuously distributed characters, our scoring system reflects an arbitrary typology.

Specimens collected from the same region more than 70 years apart showed no sign of post-mortem color change. There is some seasonal variation in coloration caused by wear. For example, in nominate *peruana*, and especially in the *fulva* group, specimens from October to June tended to be more richly colored and ochraceous than those taken from July to September. This is the only Andean forest bird with which we are familiar that shows such seasonal plumage wear.

RESULTS

Sexual dimorphism.—ANOVAs of the six skin measurements indicate a significant ($P < 0.05$) sex effect on wing-length in all subspecies except *bogotensis* (Table 1). This was also found in the analysis of specimens with skull pneumatization $\geq 90\%$. Differentiation in other characters depend on the subspecies examined. The larger sample sizes of *olivascens* and *peruana* may account for their having significant sexual dimorphism in more characters than *fulva* or *bogotensis*. Because of the apparent differences between sexes, all subsequent analyses were performed separately on males and females.

Univariate geographic variation.—Except for wing length, bill length, and mass, males and females show similar patterns of mensural character differentiation among subspecies. ANOVAs indicate that wing, tail, and tarsus lengths are significantly different among all subspecies except between *bogotensis* and *olivascens*. Other differences depend on the subspecies compared (Table 1). The elimination of specimens lacking data on skull pneumatization caused a loss of significance in those compari-

TABLE 1
MORPHOMETRIC CHARACTER MEANS WITH STANDARD DEVIATIONS^a

Character	Males			
	<i>C. o. bogotensis</i>	<i>C. o. olivascens</i>	<i>C. peruana</i>	<i>C. fulva</i>
Mass	—	25.9 ± 4.1 (15)#	*20.6 ± 1.7 (36)#	18.4 ± 2.7 (6)
Wing length	67.9 ± 0.6 (4)	69.5 ± 3.0 (42)#	*62.0 ± 1.6 (57)#	*57.9 ± 1.9 (14)#
Bill length	14.4 ± 0.7 (4)	14.1 ± 0.7 (42)	*13.3 ± 0.6 (56)#	*12.8 ± 0.8 (14)
Bill width	4.9 ± 0.1 (4)	5.2 ± 0.3 (43)	*4.8 ± 0.3 (56)	4.8 ± 0.2 (14)
Bill depth	5.1 ± 0.1 (4)	5.1 ± 0.2 (40)#	*4.7 ± 0.3 (56)	4.5 ± 0.2 (13)
Tail length	64.9 ± 1.2 (4)	65.4 ± 2.3 (41)#	*58.8 ± 1.9 (56)#	*54.9 ± 1.3 (14)
Tarsus length	25.3 ± 0.6 (4)	24.6 ± 1.3 (42)#	*23.1 ± 0.9 (55)#	*21.7 ± 1.1 (13)#
Character	Females			
	<i>C. o. bogotensis</i>	<i>C. o. olivascens</i>	<i>C. peruana</i>	<i>C. fulva</i>
Mass	—	23.0 ± 2.7 (22)#	*18.4 ± 1.3 (32)#	*14.8 ± 1.6 (10)
Wing length	68.3 ± 1.7 (5)	*65.9 ± 2.2 (52)#	*60.2 ± 2.2 (42)#	*55.3 ± 1.7 (18)#
Bill length	13.8 ± 0.1 (4)	14.0 ± 0.6 (51)	*12.8 ± 0.5 (42)#	12.6 ± 0.7 (17)
Bill width	5.1 ± 0.2 (5)	5.1 ± 0.3 (52)	*4.7 ± 0.2 (41)	4.7 ± 0.3 (18)
Bill depth	4.8 ± 0.5 (5)	4.9 ± 0.2 (49)#	*4.6 ± 0.2 (42)	4.5 ± 0.3 (16)
Tail length	62.5 ± 1.7 (5)	62.6 ± 2.5 (51)#	57.1 ± 2.1 (41)#	*53.3 ± 1.9 (18)
Tarsus length	24.4 ± 2.6 (5)	23.5 ± 1.3 (49)#	*22.4 ± 0.9 (42)#	*20.7 ± 0.8 (17)#

^a Sample sizes are in parentheses.

* Significant difference between subspecies, $P < 0.05$.

Significant difference between sexes, $P < 0.05$.

sons that were only weakly significant in the full analysis. Differences in wing length, tail length, and tarsus length remained strongly significant except in the comparison of *peruana* and *fulva*, for which tail length was no longer significantly different.

In all six size characters, *olivascens* differs significantly from its southern neighbor *peruana*. To determine whether the samples of *olivascens*

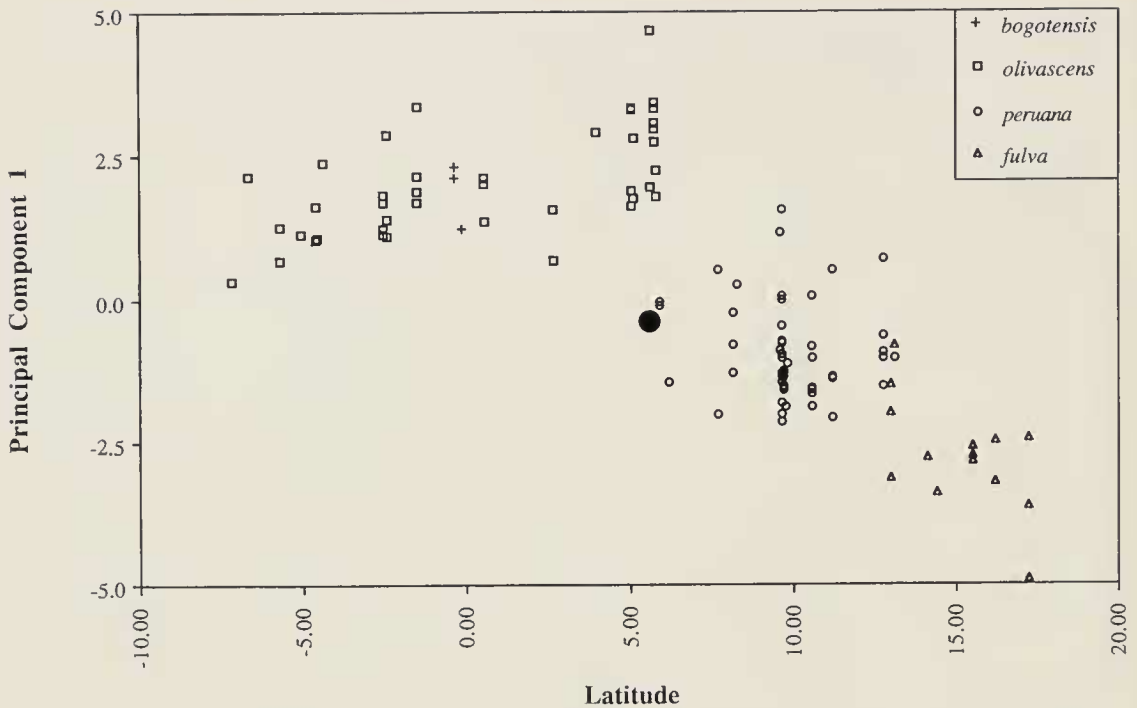


FIG. 2. Plot of first principal component axis against latitude in males. Larger circle denotes *olivascens* specimen that clusters with *peruana* (LSUMZ 88567). Negative numbers represent northern latitudes.

from north of the Equator contributed to a larger size difference between *olivascens* and *peruana* as a function of geographic distance, we used an ANOVA to compare populations of *olivascens* north and south of the equator. None of the morphometric characters showed significant differences in either sex.

A discrete size difference exists between *olivascens* and *peruana* where the two meet. Two adult *olivascens* (males: LSUMZ 117378, 11739) were taken on the east slope of the Cordillera Colán at “30 km by road E Florida on road to Rioja,” depto. Amazonas. Only 16 km SW on the west slope of Colán four adult *peruana* from “33 road km NE Ingenio on road to Laguna Pomacochas,” depto. Amazonas, were collected (males: LSUMZ 82126, 153098-9; female: LSUMZ 82125). A clue as to where the two taxa meet comes from a series taken east of La Peca Nueva. From site two, one male specimen (ca. 2680 m elev.; LSUMZ 88567; skull completely pneumatized) is *peruana* based on the morphometric characters (in multivariate space this individual sorts out with *peruana*; see large circle in Fig. 2). Although Graves (1980) considered this specimen as evidence for introgression because of a “few white feathers in the eye-ring,” it is clearly typical of *peruana* in size and plumage as well as in presence of white feathers. The other nine specimens taken from the La

Peca Nueva sites are all *olivascens* based on size, and all lack white facial feathering. This suggests sympatry between the two forms without introgression. When individual skin measurements are compared for all west slope sites, the discrete difference in size between the two subspecies is apparent (Table 2).

In both sexes, *peruana* and *fulva* differ significantly in wing, tail, and tarsus lengths. Our most northern sample of *fulva* is from a northern spur of the Cordillera Vilcabamba (depto. Cuzco, Peru), a ridge bounded on the west by the “deeply incised” Apurímac Valley (Haffer 1974). Our southernmost sample of *peruana* is only 150 km NW on a slope of the Cordillera Occidental, west of the Apurímac (Yuraccyacu, depto. Ayacucho, Peru). All specimens except one of unknown age (female: American Museum of Natural History 820507; hereafter AMNH) are clear representatives of their respective subspecies (Table 2). The aberrant specimen was taken from the Cordillera Vilcabamba and is *peruana* in tail length.

Specimens from the Cordillera Vilcabamba represent a distinctive new subspecies based on plumage (Remsen and Brumfield, unpubl. data). Because these populations are allopatric from populations of *peruana* and *fulva* from the main Andes, they are less likely to show signs of introgression between the two forms. To determine if there is any evidence of introgression between *peruana* and *fulva*, we compared the southernmost samples of *peruana* (from Yuraccyacu) with our northern most sample of *fulva* from the main Andes (males: Field Museum of Natural History 311813–4, from Pillahuata, depto. Cuzco; hereafter FMNH). Although both *fulva* specimens were typical of *fulva* in wing-length, one individual (311814) was typical of *peruana* in both tail-length and tarsus-length, two characters that are reliable for distinguishing all subspecies except *bogotensis* (Table 2). This may indicate some introgression between populations of *fulva* from the main Andes and *peruana*.

North of the equator, the elevational distribution of specimens is not correlated with latitude (Spearman $r = 0.25$, ns). South of the equator, the elevations of specimens increase slightly but significantly with distance from the equator (Spearman $r = 0.29$, $P < 0.0005$). A MANOVA revealed that there is no significant elevation effect on the morphometric characters in either sex (Wilk's Lambda = 0.07, ns).

Multivariate geographic variation.—Because individual characters do not vary independently, we performed a principal component analysis to determine which variables best account for the variation expressed across the range of the species. In specimens missing one or two characters ($N = 17$), the subspecies mean was substituted for the missing value. Eigenvalues and eigenvectors were extracted from the correlation matrix. Load-

TABLE 2
 INDIVIDUAL MEASUREMENTS OF SPECIMENS NEAR POTENTIAL CONTACT ZONES (REFER TO FIGURES 1 AND 2; SUBSPECIES MEANS ARE FOR ALL OTHER SPECIMENS)

	Mass	Wing length	Bill length	Bill width	Bill depth	Tail length	Tarsus length
Males							
<i>C. o. olivascens</i> mean	25.9 ± 4.1	69.5 ± 3.0	14.1 ± 0.7	5.2 ± 0.3	5.1 ± 0.2	65.4 ± 2.3	24.6 ± 1.3
Fig. 2, site 2	20.5	63.7	13.3	5.0	4.7	60.8	23.3
Fig. 2, site 3	29.0	76.6	16.2	5.6	5.2	71.2	25.0
Fig. 2, site 3	25.0	67.5	15.7	5.2	5.0	62.8	23.7
Fig. 2, site 4	18.0	63.7	13.5	5.2	4.7	60.0	23.8
Fig. 2, site 4	17.0	61.7	14.7	5.4	4.9	58.6	21.3
<i>C. pertuana</i> mean	20.6 ± 1.7	62.0 ± 1.6	13.3 ± 0.6	4.8 ± 0.3	4.7 ± 0.2	58.8 ± 1.9	23.1 ± 0.9
Yuraccyacu	—	61.0	13.5	5.2	4.6	59.7	23.2
Yuraccyacu	—	66.7	14.1	5.0	4.8	61.5	24.0
Yuraccyacu	—	59.0	13.5	4.8	4.9	58.9	22.7
Yuraccyacu	—	62.9	13.0	4.6	4.8	60.7	23.0
Yuraccyacu	—	60.9	13.2	4.6	4.8	57.9	22.3
Yuraccyacu	20.5	62.8	12.7	4.8	5.0	59.0	22.5
Pillahuata	19.2	58.6	13.4	5.2	4.7	57.0	24.4
Pillahuata	—	62.0	13.2	4.9	4.8	54.2	21.1
Cordillera Vilcabamba	—	59.5	12.3	4.9	4.3	55.8	21.2
Cordillera Vilcabamba	—	62.0	13.2	4.8	4.6	55.1	21.8
<i>C. fulva</i> mean	18.4 ± 2.7	57.9 ± 1.9	12.8 ± 0.8	4.8 ± 0.2	4.5 ± 0.2	54.9 ± 1.3	21.7 ± 1.1

TABLE 2
CONTINUED

	Mass	Wing length	Bill length	Bill width	Bill depth	Tail length	Tarsus length
Females							
<i>C. o. olivascens</i> mean	23.0 ± 2.7	65.9 ± 2.2	14.0 ± 0.6	5.1 ± 0.3	4.9 ± 0.3	62.6 ± 2.5	23.5 ± 1.3
Fig. 2, site 1	25.0	67.7	14.2	5.3	5.1	66.0	24.2
Fig. 2, site 1	25.5	67.9	15.4	5.6	5.4	67.4	24.4
Fig. 2, site 1	25.5	67.7	15.3	5.4	4.8	66.8	24.0
Fig. 2, site 2	25.5	68.7	14.1	5.2	5.3	65.3	24.7
Fig. 2, site 3	24.0	69.0	14.5	5.3	4.9	64.2	24.8
Fig. 2, site 3	25.0	70.0	14.4	5.2	5.3	65.4	24.2
Fig. 2, site 3	27.0	66.5	14.6	5.5	5.0	65.3	24.9
Fig. 2, site 4	15.0	59.1	13.6	4.8	4.5	56.8	21.5
<i>C. periana</i> mean	18.4 ± 1.3	60.2 ± 2.2	12.8 ± 0.5	4.7 ± 0.3	4.6 ± 0.2	57.1 ± 2.1	22.4 ± 0.9
Yuraccyacu	17.9	59.9	12.7	4.9	4.5	56.7	23.8
Cordillera Vilcabamba	—	52.8	12.4	4.5	4.5	54.4	20.8
Cordillera Vilcabamba	—	56.9	12.8	5.6	4.7	51.9	21.0
Cordillera Vilcabamba	—	55.8	12.8	5.2	4.9	53.1	19.7
Cordillera Vilcabamba	—	57.2	13.1	4.7	4.5	56.9	21.4
<i>C. fulva</i> mean	14.8 ± 1.6	55.3 ± 1.7	12.6 ± 0.7	4.7 ± 0.3	4.5 ± 0.3	53.3 ± 1.9	20.7 ± 0.8

TABLE 3
CHARACTER LOADINGS FROM PRINCIPAL COMPONENT ANALYSIS OF MORPHOMETRIC
CHARACTERS

	PCA I		PCA II		PCA III	
	Males	Females	Males	Females	Males	Females
Wing length	0.458	0.451	-0.279	-0.294	-0.133	-0.173
Bill length	0.394	0.398	0.213	-0.341	-0.781	0.628
Bill width	0.322	0.361	0.854	0.630	0.327	0.293
Bill depth	0.408	0.372	-0.040	0.544	0.272	-0.056
Tail length	0.458	0.456	-0.183	-0.321	-0.038	0.051
Tarsus length	0.393	0.402	-0.335	-0.037	0.435	-0.695
Percentage of variance	62.7	63.8	12.2	11.7	8.3	8.8

ings on the first principal component (PCA 1) are large and positive (wing-length and tail-length had the highest loadings) for all characters (this was also found in an analysis of known adults) indicating that general size accounts for most (males 63%, females 64%) of the variation (Table 3).

A regression of PCA 1 against latitude illustrates a significant negative correlation between size and latitude in males both north ($r = -0.47$, $P < 0.05$, $N = 26$) and south ($r = -0.79$, $P < 0.0001$, $N = 91$) of the equator, and in females both north ($r = -0.47$, $P < 0.05$, $N = 32$) and south ($r = -0.79$, $P < 0.0001$, $N = 85$) of the equator (Fig. 2; Table 1). It should be noted that the two taxa that occur north of the equator, *bogotensis* and *olivascens*, were represented by small sample sizes from all collecting localities (Fig. 1). Latitudinal variation within populations south of the equator is interesting in that measurements of *olivascens* are positively correlated with latitude in both males ($r = 0.50$, $P < 0.05$, $N = 21$) and females ($r = 0.50$, $P < 0.05$, $N = 24$). Populations of *peruana*, with the greatest range in latitudinal sampling, however, show no significant correlation with latitude in either males ($r = 0.26$, ns, $N = 56$) or females ($r = 0.05$, ns, $N = 42$). Finally, populations of *fulva* are significantly negatively correlated with latitude in both males ($r = -0.62$, $P < 0.05$, $N = 15$) and females ($r = -0.51$, $P < 0.05$, $N = 18$). If the subspecies examined were the result of clinal variation (i.e., not distinct evolutionary units), then we would expect size to be negatively correlated with latitude both within as well as among subspecies. The subspecies with the best latitudinal sampling, *peruana*, showed no correlation of size with latitude. More samples of *bogotensis*, *olivascens*, and *fulva* are need-

ed to allow sufficient examination of clinal variation within each subspecies.

A discriminant function analysis was used to determine the percentage of specimens that could be classified correctly solely on size measurements. This analysis is similar to PCA, but assumes *a priori* the identification of the groups based on the museum label. By making this assumption, DFA can determine which characters cause maximal separation of the groups. We plotted discriminant functions for each specimen along an axis. Specimens were considered unidentifiable if their discriminant function value overlapped with any values from their neighbor taxon. Specimens of *bogotensis* could not be distinguished from *olivascens*. When compared only to each other, 79% of *olivascens* and 92% of *peruana* were identified unambiguously. When compared only to each other, 87% of *peruana* and 73% of *fulva* were identified unambiguously. All unidentifiable specimens were examined individually for geographic proximity to their neighbor taxon and size relative to the rest of their taxon. Most unidentifiable specimens occurred far from their neighbor taxon and, therefore, probably represent extreme within-subspecies variation and not introgression from subspecific neighbors. Three of the five individuals from our most northern specimens of *fulva* (Cordillera Vilcabamba), however, could not be differentiated from *peruana* based on size measurements. These three are, however, unambiguously diagnosable based on plumage (presence of buffy-white superciliary stripe in *fulva*).

Plumage Coloration

1. *Eastern Andes of Colombia and bogotensis*.—Beginning near the northeastern extreme of latitudinal distribution of our sample, specimens examined (N = 14) from the eastern Andes of Colombia (deptos. Huila, Putumayo, and Nariño) can be distinguished from other populations in the Andes of Colombia and Ecuador by their darker, redder brown underparts. In being darker than *olivascens*, these specimens match Hellmayr's (1934) brief notes on *bogotensis*, which were described from "Bogotá" specimens that lacked precise locality data. However, we were unable to locate specimens from the possibly disjunct population (see map in Hilty and Brown 1986) farther north in deptos. Santander, Boyacá, and Cundinamarca, a region more likely to contain the true type locality for "Bogotá" specimens, as noted for this taxon in particular by Olivares (1969). Hellmayr (1934), who examined the type specimen of *bogotensis*, assigned a specimen from Andalucia, depto. Huila (presumably the same specimen in our sample, AMNH 116874) to this taxon. Therefore, we treated our sample as *bogotensis* but with some hesitancy. In any case, these specimens differ strongly from our nearest specimens from adjacent

Ecuador in depto. Napo in being a darker, richer, redder (particularly in depto. Nariño) brown on the underparts, closer to Prout's Brown or Van Dyke Brown than to the Cinnamon Brown or Saccardo's Umber of the Ecuadorian specimens, and in having much darker throats. Such levels of differentiation in color are typically accorded subspecies status.

2. *Central and western Andes of Colombia to northern Peru.*—Populations from the central Andes and the western Andes of Colombia, the eastern Andes of Ecuador, the eastern Andes of Peru north of the Marañón Valley, and some localities south of the Marañón in the eastern Andes of extreme northern depto. Amazonas, Peru, are all similar in general coloration. Their underparts are fairly dark brown, closest to Cinnamon Brown or Saccardo's Umber, with the throats slightly paler; their upperparts are an even darker brown, closest to Chestnut Brown or Van Dyke Brown, with a paler, often ochraceous-tinged forecrown. We are unable to distinguish by using any color character the specimens from the two extremes in latitudinal distribution (central Colombia vs. northern Peru), except that populations from Ecuador south to Peru show an increasing tendency towards having a trace of a postocular stripe (Table 4). Also, several specimens from Colombia have white feathering on the forehead, a feature not yet known from populations from Ecuador and Peru. These populations represent the taxon *olivascens*, the type locality of which is Santa Elena on the eastern slope of the Central Andes near the northern limit of the taxon. We found only one specimen each from the western Andes of Colombia and Ecuador. Both are within the range of color of *olivascens*.

In northern Peru, where *olivascens* meets nominate *peruana*, geographic variation in color is complex. All but one specimen from three localities in extreme northern Peru on both sides of the Marañón River are virtually indistinguishable from one another. These specimens are from (1) the Cerro Chinguela area in depto. Cajamarca, north of the Marañón (see Parker et al. 1985), (2) the Cordillera Colán area in central depto. Amazonas, south of the Marañón, and (3) the Abra Patricia area in extreme northern depto. San Martín. The only difference between the populations on opposite sides of the Marañón was a tendency towards faint postocular stripes in populations on the south side (Table 4). These represent the southernmost populations of what is currently considered *C. p. olivascens* (Fjeldså and Krabbe 1990).

However, one specimen from Cordillera Colán (ca 2680 m elev.; LSUMZ 88567; skull completely pneumatized) differs dramatically from the other 11 from the region in being paler and less reddish throughout and in having a distinct postocular streak. As noted above, it is also distinctly smaller than males from the same area (wing-length 63.7 mm

TABLE 4
 PROMINENCE OF POSTOCULAR AREA IN POPULATIONS OF *CINNYCERTHIA* Wrens in Peru
 (Numbers in Rows Refer to the Number of Specimens with Each Score)

Taxon Region ^a	Postocular score		
	0 ^b	1 ^c	2 ^d
<i>C. o. bogotensis</i>			
E. Andes	7	0	0
<i>C. o. new subspecies?</i>			
depto. Nariño	8	0	0
<i>C. o. olivascens</i>			
W. Andes (e. slope), Colombia	19	0	0
Central Andes, Colombia	7	0	0
Ecuador	14	2	0
depto. Cajamarca	15	0	0
Cordillera Colán	9	2	0
Abra Patricia	2	4	0
Total (<i>C. o. olivascens</i>)	66 (89%)	8 (11%)	0
<i>C. peruana</i>			
Cordillera Colán	0	0	1
Ne. of Ingenio; La Lejía	0	0	4
Puerta del Monte	0	0	4
depto. La Libertad	0	6	6
depto. Huánuco	1	31	2
depto. Pasco	2	23	2
depto. Junín	0	14	4
depto. Ayacucho	0	7	0
Total (<i>C. peruana</i>)	3 (3%)	81 (76%)	23 (21%)

^a Arranged from north to south.

^b 0 = No postocular stripe evident.

^c 1 = Postocular stripe inconspicuous, poorly demarcated, and probably not visible in the field.

^d 2 = Postocular stripe conspicuous, reasonably well-defined, and probably visible in the field.

vs. 72.0 mm average for other two males), and it also has an indistinct white eye-ring, a condition found in many specimens of nominate *peruana* but unknown in *olivascens*. In these respects, therefore, it matches specimens of nominate *peruana* from localities to the south. It differs, however, from nominate *peruana* from deptos. San Martín and La Libertad in being less ochraceous. As noted above, Graves (1980) considered this specimen to be an *olivascens* with signs of introgression from nominate *peruana*. However, other than being collected in the same area as true *olivascens*, it has no characters of that taxon, and its paler, less reddish coloration is not really intermediate between that of *olivascens* and

typically more ochraceous *peruana*. For those reasons, Graves (pers. comm.), with a much larger series of specimens available to him than in 1980, now considers the specimen to represent *peruana* and not an intergrade. Because *Cinnycerthia* wrens are sedentary, secretive, undergrowth-dwelling species with short, rounded wings, it seems unlikely that this individual represented a long-distance wanderer, but rather a sympatric resident population.

Three adults from "33 road km NE Ingenio on road to Laguna Pomacochas," depto. Amazonas (LSUMZ 82125-26, 153098; elevs. ca. 2315 and 2135 m), are like typical nominate *peruana* in having prominent postocular streaks (Table 4), in being a paler, less reddish brown overall, and in being small (see Morphometrics section above). One (female: LSUMZ 82125) is distinctly ochraceous on the underparts and has a white eye-ring and whitish feathers on the forehead; it is indistinguishable from nominate *peruana*. The other two (both males), however, lack the ochraceous tones and are virtually identical to LSUMZ 88567 from Cordillera Colán; one has a partial white eye-ring. The locality from which these three specimens come is just south of the main part of the Cordillera Colán and only about 10 km from localities that have typical *olivascens*. This locality, however, is also between the Cordillera Colán and a locality farther southeast, Abra Patricia, where typical *olivascens* is found. Another specimen (male: AMNH 234998) from slightly farther south at La Lejía, N. of Chachapoyas, depto. Amazonas, is slightly less reddish throughout and less ochraceous on the throat than typical nominate *peruana* from farther south, but it is more reddish throughout than the three above-mentioned specimens. We suspect that a thorough elevational transect in this region would show that, where the two taxa come together, *olivascens* will be found at high elevations and *peruana* at low elevations.

Whether the above specimens represent intermediates between *olivascens* and nominate *peruana* or whether they represent geographic variation at the northern extreme of nominate *peruana* cannot be determined without larger series of specimens, preferably accompanied by genetic samples. We currently favor the latter treatment because the specimens in question are like nominate *peruana* in size, presence of white facial feathering, and prominence of the postocular streak. The only tendency towards nominate *peruana* in the series of *olivascens* in the region is the presence of class 1 postocular streaks in some specimens (Table 4). Therefore, if there is gene flow between the populations, it is only faintly expressed in the phenotypes of the populations there. The differences between nominate *peruana* and *olivascens* are of the same general magnitude as those between *olivascens* and *C. unirufa*, which are clearly two separate species (Hellmayr 1934, Parker et al. 1985). We therefore believe

that the burden of proof falls on those who would treat *olivascens* and nominate *peruana* as a single, freely interbreeding biological species, and we regard *C. olivascens* Sharpe as a separate species. We propose "Sharpe's Wren" as an English name for *C. olivascens* and "Peruvian Wren," the name used by Hellmayr (1934), for *C. peruana*, which is endemic to Peru.

3. *Eastern Andes of central Peru*.—A series of 106 adult specimens from Puerta del Monte, depto. San Martín, south through deptos. La Libertad, Huánuco, Pasco, Junín, and Ayacucho are all relatively uniform in coloration but with some individual variation that shows little geographic pattern. Their upperparts are a dark, rich brown closest to Brussels Brown or Russet Brown but darker; most specimens have an ochraceous tinge to the forecrown. Their underparts are generally closest to Cinnamon Brown. Their throats range from buffy white to ochraceous. All but three specimens have either a class 1 or class 2 postocular streak (Table 4), and 38% (N = 41) have some white feathering on the head (Table 5). We concur with Graves (1980) that this white feathering is found only on birds with nearly or completely pneumatized skulls and that it is found in both males and females (cf. Gochfeld 1979).

4. *Eastern Andes of southern Peru and northern Bolivia*.—Reference works (Paynter 1960, Ridgely and Tudor 1989, Fjeldså and Krabbe 1990) currently treat all populations from depto. Cuzco, Peru, south to depto. Cochabamba, Bolivia, as one taxon, *C. peruana fulva*. However, this region includes at least three discrete taxa, as we outline below.

At the northern extreme in latitude of this region, specimens (N = 7) from the isolated Cordillera Vilcabamba, depto. Cuzco, differ dramatically from any other *Cinnycerthia* wren in having a well-defined dark crown. These are clearly a distinct, undescribed taxon most closely related to *C. {p}. fulva* (Remsen and Brumfield, unpubl. data). The Cordillera Vilcabamba specimens do not, however, differ significantly in any size character from *fulva* populations in Cuzco or depto. Puno, Peru, south to depto. Cochabamba, Bolivia.

The type locality of *fulva* is in the main Andes of depto. Cuzco. Unfortunately, few specimens of *fulva* have been collected in that region, and these wrens are notably rare there (T. A. Parker, pers. comm.); in fact, we can find no specimens or published localities from west of the Río Apurímac Valley through the Urubamba drainage east to at least the Río Paucartambo valley. Because humid forest in this region has been thoroughly sampled (e.g., Chapman 1921, Parker and O'Neill 1980), we suspect that the absence of *Cinnycerthia* wrens in this region may be a true gap in their distribution. In addition to the type specimen, taken at Huasampilla, we found only two other specimens in depto. Cuzco; all three are in the Río Madre de Dios drainage in the humid eastern portion

TABLE 5
 AMOUNT OF WHITE FEATHERING ON HEAD IN POPULATIONS OF *CINNYCERTHIA* WRENS IN PERU AND BOLIVIA (NUMBERS IN ROWS REFER TO THE NUMBER OF SPECIMENS WITH EACH SCORE)

Taxon Region	White head-feathering score ^a					
	0	1	2	3	4	5
<i>C. o. bogotensis</i>						
E. Andes	5	0	2	0	0	0
<i>C. o.</i> new subspecies?						
depto. Nariño	5	0	2	0	1	0
<i>C. o. olivascens</i>						
W. Andes (e. slope), Colombia	13	0	5	1	0	0
Central Andes, Colombia	5	0	2	0	0	0
Ecuador	16	0	0	0	0	0
depto. Cajamarca	15	0	0	0	0	0
Cordillera Colán	11	0	0	0	0	0
Abra Patricia	5	0	0	0	0	0
Total (<i>C. o. olivascens</i>)	65 (89%)	0	7 (10%)	1 (1%)	0	0
<i>C. peruana</i>						
Cordillera Colán	0	1	0	0	0	0
Ne. of Ingenio; La Lejía	2	1	0	1	0	0
Puerta del Monte	2	0	0	0	1	0
depto. La Libertad	8	2	0	1	1	0
depto. Huánuco	19	3	1	2	8	3
depto. Pasco	20	2	0	1	4	0
depto. Junín	13	1	0	2	2	0
depto. Ayacucho	3	0	1	2	1	0
Total (<i>C. peruana</i>)	67 (62%)	10 (9%)	2 (2%)	9 (8%)	17 (16%)	3 (3%)

TABLE 5
 CONTINUED

Taxon Region	White head-feathering score ^a					
	0	1	2	3	4	5
<i>C. fulva</i> group						
Vilcabamba (subsp. nov.)	6	0	1	0	0	0
depto. Cuzco	2	0	0	0	0	0
depto. Puno	4	0	3	1	0	0
depto. La Paz	10	0	4	2	0	0
depto. Cochabamba	6	0	0	0	0	0
Total (<i>C. fulva</i> group)	28 (72%)	0	8 (21%)	3 (8%)	0	0

^a The amount of white feathering on the head (in *fulva*, excluding the superciliary) was scored as: (0) none; (1) partial or complete, small, white eye-ring; (2) a portion of the forehead with white feathers; (3) both 1 and 2; (4) extensive white feathering on face and forehead; or (5) much of the head white, especially most of the face and crown.

of the departamento. The two specimens that we examined (FMNH 311813–814, from Pillahuata) are extremely similar to each other and differ dramatically from specimens from depto. Puno, Peru, to depto. Cochabamba, Bolivia, in having a superciliary that is less conspicuous because it is ochraceous rather than buff-white, and because it is not as broad. Also, the broad, dark eye-line is less conspicuous because the auriculars are much darker, and the back and underparts are slightly darker. In these features, the Cuzco specimens could be regarded as showing variation in the direction of *peruana*. We suspect that this is why Paynter (1960) merged *fulva* into *peruana*. Even if the gap in distribution in western depto. Cuzco is a sampling artifact, *peruana* would be separated from *fulva* by the canyon of the Río Urubamba, and so no test of sympatry is possible for direct assessment of species limits. Therefore, whether *peruana* and *fulva* should be treated as different biological species depends on the importance one assigns to the apparent variation towards *peruana* shown in Cuzco specimens of *fulva*.

We propose that *fulva* be elevated to species status because *fulva*, particularly those populations from the Cordillera Vilcabamba and those from depto. Puno south, differs in plumage pattern more than *peruana* does from *C. olivascens* or than even *C. olivascens* does from *C. unirufa*. All populations currently included in *fulva* differ from *C. peruana* in having a distinctive, well-defined superciliary that extends from the forehead at the nares posteriorly to the nape. The auriculars are pale like the superciliary, thereby sharply demarcating a broad, dark eye-stripe, and the auriculars are only slightly darker than the pale throat. Thus, *fulva* has a patterned face, with a conspicuous pale superciliary and dark eye-stripe, whereas *peruana*, which only occasionally has a hint of a post-ocular superciliary on an otherwise uniform reddish-brown face, has no face pattern. The head pattern of *fulva* gives the bird a different “look” from *C. peruana*, a difference that doubtless led to these populations’ original placement in a different genus, *Thryophilus* (now merged in *Thryothorus*). As noted by Ridgely and Tudor (1989), the face pattern of *fulva* recalls that of the sympatric Mountain Wren (*Troglodytes solstitialis*). The rest of the plumage, however, is similar to other *Cinnycerthia* species. The breast and belly, closest to a pale dull Sayal Brown, are paler and less reddish than those of *C. peruana*. The upperparts are like those of *C. peruana* but are also paler and slightly less reddish. Finally, the extensive white feathering found in some *peruana* is unknown in *fulva* (Table 5). We propose that Hellmayr’s (1934) English name for *fulva*, “Superciliated Wren,” be used for this species. We suspect that comparisons of vocalizations will be especially important in resolving species

limits; T. A. Parker (pers. comm.) has observed that *fulva* is rather quiet compared to the often noisy *peruana*.

The distinctively small, pale specimens from depto. Puno, Peru, and deptos. La Paz and Cochabamba, Bolivia, seem to be indistinguishable from one another in plumage or size; the paleness of a recent LSUMZ series of 13 July-August specimens from the Chuspipata region of La Paz seems attributable to seasonal wear. The Puno-to-Cochabamba population represents an undescribed subspecies (Remsen and Brunfield, unpubl. data) that differs from the depto. Cuzco population in the ways described above.

Although white facial feathering has been reported in *C. peruana sensu lato* from Ecuador south (Fjeldså and Krabbe 1990), we cannot find any explicit reference to such white feathering in *fulva*. In a series of 39 adults of *fulva* from depto. Puno to depto. Cochabamba, eight individuals show "extra" white feathers on the forecrown above the superciliary and three of these have "extra" white feathers around the eyes (Table 5); none, however, shows the class 4 or class 5 white feathering found regularly in *peruana*.

DISCUSSION

Zoogeography.—Somewhere in the Eastern Andes of extreme northern Ecuador or southern Colombia, *bogotensis* must meet *olivascens*. We know of no geographic barriers in the region that might separate the two. The southern limit of *olivascens* also does not correspond to any prominent geographic boundary. The deep, arid Marañón valley has long been recognized as a major barrier to dispersal for birds occurring in humid montane forest. Parker et al. (1985) noted 18 pairs of allospecies separated by the Río Marañón. However, *C. olivascens* is found on both sides of the barrier, and our limited samples suggest that it interdigitates with *C. peruana* in the Andes just south of the Marañón. The southern limit of *peruana* corresponds to one of the most important biogeographic boundaries in the humid Andes, the Río Apurímac valley (Haffer 1974).

The distinctive new subspecies of *fulva* in the Cordillera Vilcabamba adds another taxon endemic to this major outlying range. The gap in distribution between the distinctive taxon in the Cordillera Vilcabamba and the range of nominate *fulva* in southeastern depto. Cuzco is a pattern also found in the Rufous-naped Brush-Finch (*Atlapetes rufinucha*) (Remsen 1993).

Nominate *fulva* and the undescribed southern subspecies must meet somewhere in southern depto. Cuzco or northern depto. Puno. Several other pairs of Andean bird taxa share this pattern (e.g., Marcapata Spinetail [*Cranioleuca marcapatae*] and Light-crowned Spinetail [*C. albi-*

ceps], Remsen 1984b; White-throated Spadebill [*Platyrinchus mystaceus zamorae* and *P. m. partridgei*], Remsen et al. 1991). Precisely where this turnover takes place is not known, but the most likely geographic barrier in the region is the Río Marcapata valley in extreme southeastern depto. Cuzco.

Species limits.—Our analysis of geographic variation in plumage and morphology in populations currently treated as *Cinnycerthia peruana* supports recognition of three biological species. The northernmost, *olivascens*, shows large, discrete morphometric differences from the next population to the south, *peruana*, as well as marked plumage differences. Some specimens in the region of contact, however, have intermediate plumage characters that could be interpreted as evidence of past or present gene flow. The presence of these two different forms in such geographic proximity suggests that either an abrupt step cline serves to differentiate the groups or, more likely, past geological events (e.g., Río Marañón) isolated the forms long enough for differentiation to occur. The absence of unambiguously intermediate forms and the presence of an individual of *peruana* within a population of *olivascens* suggest that these two taxa are best treated as separate but closely related species.

Although contact between *peruana* and *fulva* is prevented by the Apurímac Valley, the distinctive plumage pattern of *fulva* relative to other *Cinnycerthia* species suggests that *fulva* should be treated as a separate species; in fact, no reason was ever published for the merger (by Paynter 1960) of *fulva* into *peruana*.

In summary, we recommend the following taxonomic treatment:

Cinnycerthia olivascens Sharpe's Wren

C. o. bogotensis (eastern Andes of Colombia)

C. o. olivascens (central Andes and western Andes of Colombia, eastern Andes of Ecuador, eastern Andes of Peru south extreme northern depto. Amazonas, Peru)

Cinnycerthia peruana Peruvian Wren (eastern Andes of Peru from depto. Amazonas to depto. Ayacucho)

Cinnycerthia fulva Superciliated Wren

C. f. (undescribed subspecies) (Cordillera Vilcabamba, depto. Cuzco, Peru)

C. f. fulva (eastern Andes of depto. Cuzco, Peru)

C. f. (undescribed subspecies) (depto. Puno, Peru, to depto. Cochabamba, Bolivia)

Bergmann's Rule.—The linearity of the distributions of Andean forest birds (Remsen 1984a, Graves 1988) creates a unique opportunity to assess

Bergmann's Rule, which predicts that the body size of organisms increases in colder and drier areas as a response to changes in climatic conditions (James 1970). Although climatological data are unavailable for the humid Andes, we assume that temperatures in the Andes are colder with increasing distance from the Equator; rainfall data from LSUMZ collecting localities in Peru and Bolivia also suggest that localities farthest from the equator are drier. The elevational distribution of our specimen localities remains constant over latitude north of the Equator and increases with latitude south of the equator. Therefore, we do not believe that elevation per se is a variable that would influence body size, or if so, the influence would be in producing colder temperatures with increasing elevations south of the Equator.

Although Bergmann's Rule, including both the pattern and the explanation for the pattern (James 1970), seems deeply entrenched in vertebrate biology, 68% of the studies on intraspecific variation compiled by Peters (1992) do not support the rule (see also McNab 1971, Zink and Remsen 1986, Geist 1987). Only four studies have investigated Bergmann's rule in Andean birds. Graves (1991) found a positive correlation between body size and latitude in the Carbonated Flowerpiercer (*Diglossa carbonaria*) in both directions away from the equator, as did Kratter (1993) for the Yellow-billed Cacique (*Amblycercus holosericeus*). Remsen et al. (1991) found that body size in the White-throated Spadebill (*Platyrinchus mystaceus*) decreased south of the equator, counter to the prediction of Bergmann's rule, but the analysis included only populations south of the equator. Additionally, Remsen (1993) found that body size decreased away from the equator in *Atlapetes rufinucha*, but only those populations from depto. Cuzco (13°S. Lat.) to depto. Santa Cruz, Bolivia (18°S. Lat.) were analyzed. Although Bergmann's Rule is intended to apply primarily to intraspecific variation, we believe that its application to allopatric sister-species (allospecies), as in the *Cinnycerthia* populations analyzed herein, is also appropriate. Our results indicate that body size is negatively correlated with latitude in *Cinnycerthia* wrens both north and south of the equator, counter to Bergmann's Rule. The only exception appears within populations of *olivascens* south of the equator, where size may be positively correlated with latitude. Obviously, congruence between large numbers of a wide variety of taxa is necessary to determine the applicability of Bergmann's "Rule" to Andean birds.

ACKNOWLEDGMENTS

We thank the curatorial staffs of the Academy of Natural Sciences of Philadelphia, American Museum of Natural History (New York), Carnegie Museum of Natural History (Pittsburgh), Field Museum of Natural History (Chicago), and Delaware Museum of Natural

History (Dover) for generous loans of specimens. We thank A. P. Capparella, R. T. Chesser, J. C. Coulson, G. R. Graves, A. W. Kratter, T. S. Schulenberg, D. A. Wiedenfeld, and two anonymous reviewers for providing helpful comments on the manuscript. G. R. Graves re-examined material from northern Peru. J. M. Bates, S. J. Hackett, T. A. Parker III, K. V. Rosenberg, and T. S. Schulenberg provided to RTB immeasurable help and encouragement in the project's development. S. A. Juliano assisted with statistical analyses. The morphometric analyses of this paper initially were prepared by RTB as a research project for JVR's ornithology course.

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